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The effect of cross-boundary management on the trajectory to commonness in biological invasions

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Abstract

The number of alien species introduced and undergoing range expansion in novel environments is steadily increasing, with important consequences for native ecosystems. The efficacy of management planning and decision making to limit such invasions can be improved by understanding how interventions will impact the population dynamics of recently introduced species. To do so, here we expand on a typological framework that enables the classification of populations over time into 10 categories of commonness, and apply it to a spatially discrete metapopulation with heterogeneous abundance across spatial units (patches). We use this framework to assess the effect of cross-boundary management on the capacity of a metapopulation with different demographic and dispersal characteristics, including time lags in population growth, to become common. We demonstrate this framework by simulating a simple theoretical metapopulation model capable of exploring a range of environments, species characteristics, and management actions. Management can vary in the efficacy of propagule interception between patches, and in the synchronisation of the implementation of these measures across patches (i.e. if management is implemented simultaneously across patches). Simulations show that poor interception efficacy that only modestly reduces the number of propagules entering a given spatial unit cannot be compensated for by strong management synchronisation between spatial units. Management synchronisation will nonetheless result in a reduction in rates of spread once a critical threshold of interception efficacy has been met. Finally, time lags in population

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growth that may result in delayed spread are an important aspect to be considered in management as they can amplify the efficacy of management. Our results demonstrate how a typological framework of categories of commonness can be used to provide practical insights for the management of biological invasions.

Keywords
Abundance, alien species, allee effect, biosecurity, occupancy, simulation model, spread, time lags

Introduction

The number of species becoming established in regions outside their native range is rapidly increasing as a result of human trade and transport (Seebens et al. 2017). This rapid accumulation of alien species is troublesome as biological invasions constitute a major threat to biodiversity, local economies and human welfare (McGeoch et al. 2010; UNEP CBD 2010; Bellard et al. 2016). Cross-border biosecurity measures focussed on prevention of introductions are most effective at limiting invasions (Hulme 2009; Hulme et al. 2009; Scalera et al. 2016; IUCN 2018), in combination with the management of populations of alien species that are already established (Martin et al. 2020). A combination of both approaches can also be used to prevent the secondary spread of an introduced species across spatial units, such as water bodies or conservation areas (Vander Zanden and Olden 2008). Cooperation between countries is also crucial to control biological invasions and prevent efforts from one country to control a given species to be undermined by the lack of action of others where the species is present (Genovesi 2011; Faulkner et al. 2020). The resources and self-interests of different countries can nonetheless affect the degree of cooperation.

Quantifying both the local abundance and area of occupancy of alien populations is important to assess and track how a species newly introduced into a novel environment may spread (Catford et al. 2016; McGeoch and Latombe 2016). Considering local abundance separately from the distribution is crucial to implement appropriate management responses, as different actions will be more or less efficient over large regions and small or large populations. For alien species that have recently been introduced, the residence time is also of utmost importance, as it will influence the urgency and efficacy of management actions, with species spreading rapidly being of particular concern (McGeoch and Latombe 2016). Residence time also provides important information on management feasibility (Brock et al. 2020). Taken together, these three dimensions (local abundance, area of occupancy, residence time) can be combined following a typological approach into eight discrete categories of commonness for alien species (Fig. 1; see also table 1 in McGeoch and Latombe 2016). In this typology, local population size can be small or large, geographic range can be narrow or wide, and residence time can be short or long. A newly introduced alien species with low abundance over a narrow range ('Newly established') can become more common, i.e. being abundant over a wide region after some time ('Successful'), by transiting over time through different categories of commonness (e.g. by first increasing its abundance locally before

a)

Category	Local Population Size		Geographic Range	Residence Time
	Local Mean Abundance	Maximum Local Abundance	Area of Occupancy	
Newly established	Small	Small	Narrow	Short
Incipient	Large	Large	Narrow	Short
Dispersed	Small	Small	Wide	Short
Dispersed + Abundant somewhere	Small	Large	Wide	Short
Highly successful	Large	Large	Wide	Short
Not common	Small	Small	Narrow	Long
Constrained	Large	Large	Narrow	Long
Sparse	Small	Small	Wide	Long
Sparse + Abundant somewhere	Small	Large	Wide	Long
Successful	Large	Large	Wide	Long

b)

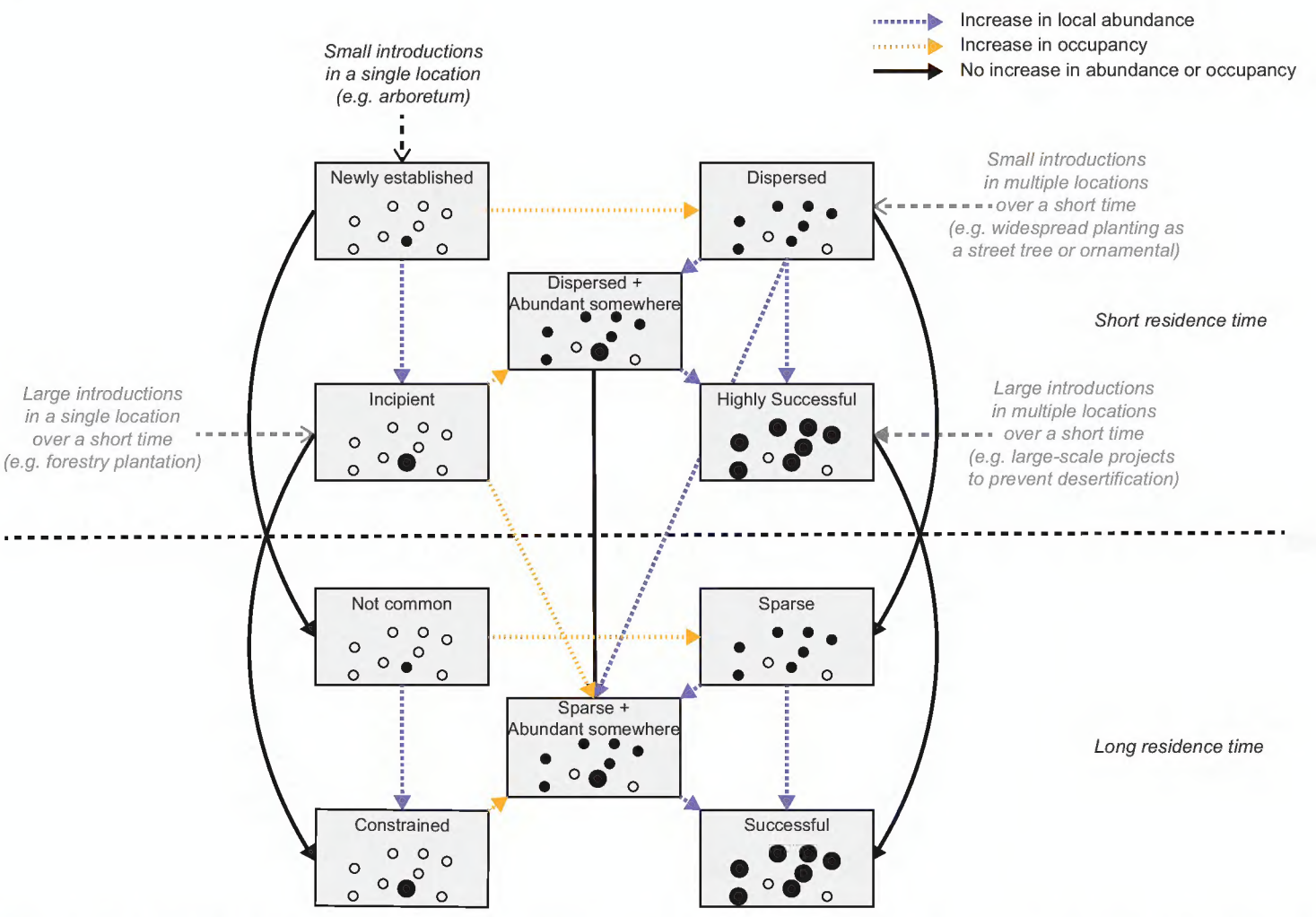
Increase in local abundance
Increase in occupancy
No increase in abundance or occupancy
Small introductions in a single location (e.g. arboretum)
Newly established
Dispersed
Small introductions in multiple locations over a short time (e.g. widespread planting as a street tree or ornamental)
Dispersed + Abundant somewhere
Short residence time
Large introductions in a single location over a short time (e.g. forestry plantation)
Incipient
Highly Successful
Large introductions in multiple locations over a short time (e.g. large-scale projects to prevent desertification)
Not common
Sparse
Sparse + Abundant somewhere
Long residence time
Constrained
Successful

Figure 1. Schematic showing the different trajectories to commonness for alien species described by a typological approach based on ten categories. **a** For a metapopulation in a network of discrete patches, abundance can be spatially heterogeneous, and both local mean abundance (LMA) and maximum local abundance (MxLA) must be used to capture all the potential trajectories to commonness (see text explanation). Using LMA only to quantify local population size can underestimate the commonness of a metapopulation. This results in the creation of two new categories in addition to the original eight categories from McGeoch and Latombe (2016): 'Dispersed + abundant somewhere' and 'Sparse + abundant somewhere'. **b** A population can transit from one category to another by increasing its abundance (blue arrows – large circles) or range (yellow arrows) rapidly, or by remaining at similar abundance and range levels over a long period of time (black arrows). When both abundance and range increase rapidly at the same time, some categories may be skipped (e.g. transit directly from 'Newly established' to 'Dispersed + abundant somewhere'). Arrows that cross or are under the dashed line indicate changes in abundance or occupancy that occur after a time lag.

dispersing). The sequence of categories will depend on the species' demographic and dispersal characteristics, but also on stochastic effects, lag phases, etc. It is important to note that these categories should not be seen as having hard boundaries for species or populations in space or time. Rather, they are a useful typological approach to better understand and conceptualise the variable ways in which species expand their ranges (and in some situations eventually contract them), and potentially identify management strategies that are more or less effective in each case.

The potential for a newly introduced alien species to become abundant will be determined mostly by its local population growth rate, whereas its capacity to become widespread will be determined primarily by its dispersal rate, and both can be influenced by humans. Newly introduced populations are often assumed to exhibit logistic growth, although many factors can affect population growth, from the relationship between density and per capita population growth to the influence of the local spatial structure on encounters between organisms (Law et al. 2003; Mistro et al. 2012). Population growth can also be reduced by multiple mechanisms associated with small population size leading to time lags caused, for example, by Allee effects (Courchamp et al. 1999; Stephens et al. 1999; Berec et al. 2007), or the time required for genetic or phenotypic adaptations to the new environment (Pérez et al. 2006). Such time lags in population growth imply that newly introduced populations may remain at low density and have a restricted range for some time, before growing and spreading across regions (Mistro et al. 2012; Essl et al. 2015; Rouget et al. 2016; Hui and Richardson 2017).

Species dispersal, the mechanism directly responsible for range expansion, is affected by a wide variety of factors, from species' physical traits, behaviours and movements to the presence of natural and human-mediated vectors, as well as properties of the local environment (e.g. connectivity) (Nathan et al. 2012). At a given spatial scale, dispersal can be considered to range from (1) diffusion processes (usually natural), (2) dispersal involving long-distance dispersal events (either through natural processes or human mediation), and (3) stratified diffusion explicitly representing two different spatial scales (Wilson et al. 2009; Lewis et al. 2016; McGeoch and Latombe 2016). Even human-mediated dispersal can encompass a wide variety of vectors with different dispersal characteristics within a network of connected locations (e.g. Seebens et al. 2013; Banks et al. 2015). Long-distance dispersal, either natural or by human agency, is a key factor responsible for dramatic increases in the spread and invasion success of alien species (Lewis et al. 2016; Hui and Richardson 2017). Abundance and dispersal are not independent phenomena, thus understanding how the combination of different growth and dispersal rates affect the abundance and range of species is necessary to capture the complexity of the different ways in which a species can become more common (McGeoch and Latombe 2016).

Here, we simulate the effect of cross-boundary management of a theoretical species on a network of discrete, interconnected patches randomly distributed in space, exchanging propagules with each other through human mediation (i.e. a metapopulation). We analyse (1) how variations in interception efficacy (the proportion of propagules from the simulated species that get intercepted when migrating from one patch

to another) and (2) management synchronisation between patches affects the trajectories of how alien species become more common under different demographic and dispersal characteristics. Here management synchronisation represents the simultaneity in the implementation of management measures across patches. Once these measures start being implemented in a patch, low synchronisation therefore corresponds to a delay before they start being implemented in other patches. In real systems, lack of synchronisation can be driven by differences in priorities, for example if different countries consider an alien species to be more or less harmful. Practical limitations also play a role when, for example, resources to implement management measures across, for example, water bodies, are logistically difficult or costly. We focus on cross-boundary management, and do not consider within-patch management of alien populations in the model. We first outline the categories of commonness constituting the typological approach, and the mechanisms through which a population can transit from one category to another, i.e. the trajectory to commonness (*sensu* McGeoch and Latombe 2016). We show how the original classification into eight categories must be extended to consider ten categories, to account for the spatial heterogeneity in local abundance. We then assess how the trajectory to commonness is affected by (1) various demographic characteristics and dispersal rates, and (2) the interception efficacy and the synchronisation of cross-boundary management across patches. This is particularly relevant in the context of legislation that is implemented by groups of countries, such as the European Union IAS regulation 1143/2014 (EU 2014).

We predict that stronger synchronisation in the implementation of cross-boundary management in different patches and higher interception efficacy should limit the ability of a metapopulation to increase its area of occupancy across the network of patches. This will prevent it from reaching categories of commonness characterised by large areas of occupancy. We expect that synchronisation is important for preventing alien species with good long-distance dispersal abilities from establishing in new patches before cross-boundary management is implemented. By contrast, we expect that interception efficacy plays an important role in spread to new patches for all alien species. Finally, we anticipate that time lags will make the efficiency of cross-boundary management less dependent on the synchronisation of cross-boundary managements.

Methods

Categories of commonness and mechanisms of transition between categories

Species range sizes are typically assessed using either the extent of occurrence (the total continuous area over which the species occurs) or the area of occupancy (AoO, the area within the extent of occurrence over which a species occurs, for a given spatial grain) (IUCN 2001). Here, we use the AoO for a network of discrete patches of equal size, randomly distributed in space, as it is independent of the spatial distribution of patches, contrary to the extent of occurrence.

Across a network of discrete patches, the abundance of populations occupying different patches will be heterogeneous. To obtain a single summary measure of abundance over a set of independent patches that is independent from AoO, the local mean abundance (LMA), computed as the mean abundance of occupied patches (i.e. discarding empty patches in the computation, otherwise LMA becomes simply proportional to the overall abundance) is used (Gaston et al. 2000; McGeoch and Latombe 2016). However, LMA decreases when new populations with low local abundance establish, which can result in the metapopulation being considered as less common than before. This is logically incorrect, since the species has spread without becoming less abundant overall. In such a situation, abundance has only become spatially heterogeneous. To prevent this logical fallacy and account for the spatial heterogeneity in abundance, two additional categories of commonness are needed: 'Dispersed + abundant somewhere' and 'Sparse + abundant somewhere' (Fig. 1). Here the maximum local abundance (MxLA) of the metapopulation is quantified, as it will not change simply from averaging multiple population abundances. If a metapopulation includes abundant populations in a small number of patches, both the LMA and the MxLA will be large. If a small number of propagules spreads to other patches, the LMA will decrease and can become small, whereas the MxLA will remain high, capturing the constant abundance in the source patches. Species can have different growth rates and dispersal characteristics across a region, and AoO, LMA and MxLA will therefore change over time across the multiple discrete patches (see Suppl. material 1: Appendix A for different archetypes of trajectories to commonness).

The metapopulation model

We apply the analyses in a model system consisting of 20 dimensionless patches with the same carrying capacity, randomly distributed in space in a square region of 100 × 100 distance units. Such patches can intuitively represent entities such as islands, water bodies, or national parks, for which a number of cross-border management measures exist (Kaplan and White 2002; Kark et al. 2015; IUCN 2018). The metapopulation concept can also be extended to represent countries exchanging propagules, whose spatial scale is the one on which biosecurity legislation and measures are more commonly designed and implemented. The distance between patches can then be considered as a proxy to represent differences in the movements of propagules between patches resulting from various pathways between countries, such as the amount of trade and people movements. Patches were at least five distance units from each other. While the size of the chosen model system is arbitrary, it is within the range of realistic cases. For example, the number of countries per continent ranges from 14 to 58, and there are 27 member states in the European Union. Each patch had a carrying capacity of K = 10,000 individuals. The population dynamics follows logistic growth:

$$N_{t+1} = round\left(N_t + r \times N_t \times \left(1 - \frac{N_t}{K}\right)\right) \quad \text{Eq. 1}$$

Table 1. Model parameters and their values. All parameters are combined in models, the only exception being the two dispersal kernels that are used separately from each other.

Parameter name		Parameter symbol	Definition	Parameter values
Population model core parameter		r	Per capita growth rate	0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1
Allee effect		A	Value of the Allee effect (used to model time lag). A low value indicates a high time lag.	Ø , 0.3 (weak Allee effect), -0.001 (strong Allee effect)
Dispersal parameter	*– Gaussian*	σ	Standard deviation of the Gaussian distribution. Represents dispersal rate.	5, 6, 7, 8, 9, 10
	– Cauchy	γ	Scale parameter of the Cauchy distribution. Represents dispersal rate.	0.5, 1.1, 1.7, 2.3, 2.9, 3.5
Synchronisation of cross-border management		s	Number of time-steps (i.e. time) before a new patch starts implementing cross-boundary management. At the most extreme values of s relatively few patches will begin border measures within the time horizon of the simulations. Represents synchronisation.	0, 1, 5, 10, 15, 20
Intensity of cross-border management		i	Proportion of immigrating individuals that are eliminated at each time-step. Represents the interception efficacy of the cross-boundary management.	0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9
Simulation ID		Ø	ID of the simulation run, characterised by a random spatial distribution of patches. For a given ID, the spatial distribution of patches remains the same when varying the other parameter values.	1, … , 20
Other parameters with fixed values across simulations		K	Carrying capacity of each patch	10000
		Ø	Number of patches	20
		Ø	Size of the square area	100 × 100 (dimensionless)
		Ø	Minimum distance between two patches	5 (dimensionless)
		Ø	Number of time steps per simulation	200

where r is the per capita growth rate, which varies between 0.1 and 1 (Table 1). Here we use the model in a theoretical context to explore how relative changes in demographic and dispersal characteristics would qualitatively impact the trajectory to commonness of a metapopulation that is, by default, constantly increasing and spreading. Therefore, the values of the carrying capacity and of the number of patches is arbitrary, although the orders of magnitude reflect real systems. We nonetheless ran preliminary analyses to assess the effects of varying these parameters. Simulations with $K = 100$ showed qualitatively similar results, although a larger carrying capacity provided advantages to populations that were able to disperse over long distances because of the increase in number of propagules. Similarly, using more than 20 patches would provide more dispersal opportunities between patches, and as a result the speed at which an alien species would become common is likely to increase.

Patches were initialised with zero individuals of the focal alien species, except for one randomly selected patch, which is initialised with 500 individuals (Suppl. material 1: Fig. B1 in Appendix B). At each time-step, two events occurred: (i) the population of each patch grew following Eq. 1, and (ii) a proportion of the population migrated to other patches with a probability determined by a distance-based gravity model using dispersal kernels. For every focal patch, all patches (including itself) received a score based on the distance between their centres and the focal patch's centre, computed from the chosen dispersal kernel (described below). The scores were then divided by the sum of scores to determine the proportion of propagules from the focal patch ei-

ther remaining in the focal patch or migrating to another one. That is, each propagule leaving a focal patch necessarily reached another patch. That implies that at each time-step, patches lose individuals due to emigration, and gain others from immigration. If emigration was higher than immigration (which would happen for patches with disproportionately high abundance compared to other patches), the population of the patch decreased, in a classic source-sink dynamic (but this decrease was compensated by local population growth).

The effect of different types of dispersal was compared by running the gravity model with either a Gaussian kernel (Eq. 2) or a Cauchy kernel (Eq. 3) (Suppl. material 1: Fig. B2 in Appendix B). Different dispersal kernels (and combinations of kernels) can be used to model the spread of a population, but the Gaussian and Cauchy distributions represent two extremes (McGeoch and Latombe 2016) (although another trivial extreme case would be a uniform distribution, in which case the metapopulation would simply be equivalent to a single population). Gaussian kernels are typically used to model simple diffusion for which long-distance dispersal is extremely rare. Here we use it to represent a situation in which a population will spread in a network by primarily invading neighbouring patches. The Cauchy kernel is commonly used to model frequent long-distance dispersal events due to having a very fat tail (Nathan et al. 2012; Lewis et al. 2016). Here we use it to represent frequent dispersal between patches distant from each other. The Cauchy dispersal has a narrower peak than the Gaussian kernel, implying that more propagules will remain in a given patch, although the fat tail means that the propagules emigrating from a patch can do so over longer distances. These two kernels also offer the advantage of being characterised by a single parameter (contrary to stratified dispersal and many other fat-tail kernels), simplifying simulation analyses.

$$G(d) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{\frac{-d^2}{2\sigma^2}} \quad \text{Eq. 2}$$

$$C(d) = \frac{1}{\pi\gamma\left[1+\left(\frac{d}{\gamma}\right)^2\right]} \quad \text{Eq. 3}$$

where d is the distance between the centres of two patches, and σ and γ represent the dispersal rate of the individuals (Table 1; Suppl. material 1: Fig. B2 in Appendix B).

The model was run for 200 time-steps for each replicate. That enabled the averaged abundance across the 20 patches to reach at least 9500 individuals, except for at the lowest growth and dispersal rates. 20 replicates were run for each set of parameter values (Table 1). For each replicate, a new random spatial configuration of the patches was used (Suppl. material 1: Fig. B1 in Appendix B).

In addition, we implemented time lags using weak and strong Allee effects to explore the consequences of time lags in population growth on the efficacy of cross-boundary management (Taylor and Hastings 2005; Berec et al. 2007; Hui and Richardson 2017). Species with a weak Allee effect can be especially problematic in practice, as they may remain undetected locally for a long time while spreading in other

patches before increasing in abundance, but this time lag in return can enhance the efficiency of proactive management measures. The Allee effects were modelled using the following equation:

$$N_{t+1} = round\left(N_t + r \times N_t \times \left(1 - \frac{N_t}{K}\right) \times \left(\frac{N_t + A*K}{K}\right)\right) \quad \text{Eq. 4}$$

A was set to 0.3, a value similar to those used in other studies (García-Díaz et al. 2019), for the weak Allee effect. A was set to -0.001 for the strong Allee effect, because preliminary simulations showed that higher values would prevent the metapopulation from spreading (see Suppl. material 1: Fig. B3 in Appendix B for the effect of changing the value of parameter A on the growth rate of a population).

Cross-boundary management

To model cross-boundary management between patches, we restricted immigrating propagules to successfully reach a patch with a probability i (varying from 0.1 to 1; Table 1). Migrating propagules had a probability $1 - i$ of being eliminated. This probability, which represents the efficacy of cross-boundary management, was identical for all patches in a simulation. The number of individuals reaching a patch at distance d from a source patch is therefore on average $N(t) \times i \times G(d)$ or $N(t) \times i \times C(d)$. By setting $i > 0$, we consider that management will only ever be partial, as results would be trivial otherwise. Although full containment is approachable in some cases (e.g. Bailey et al. 2011), achievable efficacy depends on the species and life forms considered (Panett and Cacho 2012). Note that we did not include any management affecting the local abundance within patches, to isolate the effect of cross-boundary management.

To represent challenges linked to relative differences in the effective implementation of legislation in different countries and levels of cooperation between them, we introduced the synchronisation term s between patches in the model. s represents the time delay after which cross-boundary management starts being implemented in a new patch (i.e. the opposite of synchronisation). Once a given patch starts applying cross-boundary management, it applies for the rest of the simulation. Setting the time delay s to 0 represents perfect synchronisation. We then ran simulations so that during every s time-step, a new random patch starts implementing cross-boundary management, until all patches apply cross-boundary management (with s ranging from 1 to 20; Table 1). The values for i and s were chosen to cover a range that was large enough to observe some effects on the modelled populations' path to commonness using this theoretical model. In practice synchronisation therefore represents differences in the existence of suitable legislation, or in the effectiveness of implementation of cross-border biosecurity legislation across countries for a given species, as different countries or regions can have different priority species. By varying i and s, we therefore explore the efficiency of different types of cross-border management in reducing the time and trajectory by which a species becomes abundant in all patches for different local population growth rates and rates of spread between patches.

Computation of the categories of commonness

For assessing the path to commonness of a metapopulation in a given simulation using the categories of the framework, the outputs of all time-steps of the 20 replicates were used without implementing any cross-boundary management or time lag (i.e. 200 × 20 = 4000 sets of values) for each dispersal kernel; we applied the following thresholds: a metapopulation changed category if the population of an occupied patch reached three quarters of the carrying capacity on average (i.e. LMA or MxLA > 7500), if more than three quarters of the patches were occupied (i.e. AoO > 15), or if residence time reaches half the number of time-steps. Since in our model a metapopulation necessarily becomes more common as time passes, increasing the number of time-steps during a simulation results in more time-steps for which maximum AoO, LMA and MxLA are attained, which artificially increases the number of time-steps for which the metapopulation is classified as 'Highly successful' or 'Successful'. Therefore, only the first 100 time-steps for each simulation were used to better show the effect of varying the parameter values on the path to commonness, setting the residence time threshold to 50 time-steps. This combination of thresholds enabled all categories of commonness to be represented in the simulations, and enabled us to better discriminate the effect of the different model parameters on the simulation outputs. For each simulation, the proportion of the number of time-steps spent in each category of the 100 time-steps was computed. This proportion was then averaged over the 20 replicates of each parameter combination and used to assess the path to commonness for each combination of parameter values.

Relative effect of cross-boundary management with and without time lag

We assessed if the effect of cross-boundary management was higher in the presence of an Allee effect compared to logistic growth, i.e. if cross-boundary management changes the time spent in a category more when a time lag is present. First, we compared the time (number of time-steps) spent in a category of commonness with and without cross-boundary management, using the following formula (the 'sparse' category is used here as an example):

$$prop\_rel(Sparse, i \neq 0, s \neq 0) = prop(Sparse, i \neq 0, s \neq 0) \times \frac{1 + prop\ (\ Sparse\ , i \neq 0, s \neq 0)}{1 + prop\ (\ Sparse\ , i = 0, s = 0)} \quad \text{Eq. 5}$$

This formula prevents divisions by 0 when a metapopulation did not reach the category without cross-boundary management ($i = 0$, $s = 0$). It also gives the same result (0) when a metapopulation did not reach the category with cross-boundary management for different ($i \neq 0$, $s \neq 0$) combinations, regardless of the outcome without cross-boundary management. A low value indicates that the metapopulation spends less time in the category when cross-boundary management is applied (the values are bounded between 0 and 0.75).

Eq. 5 was applied to the logistic growth and the Allee effects separately, and the difference *prop_rel_Allee*() – *prop_rel*() was then computed. A positive difference indicates that the proportion of time spent in a category of commonness increased following application of cross-boundary management when a time lag was applied relative to the logistic growth, whereas a negative difference indicates that this proportion decreased. In other words, non-zero values indicate that, for the same intrinsic growth and dispersal rates, time lag enhanced the effect of cross-boundary management.

Results

Trajectories to commonness under different demographic and dispersal characteristics in the absence of cross-boundary management

During a simulation run, metapopulations transited through different categories of commonness, with the specific sequence depending on the spatial distribution of patches. Fig. 2 shows how, for a given combination of parameter values, a metapopulation changed from one category to another as time passed, with differences between spatial distributions indicated by differences in the time step at which transitions occurred. To summarise these results, the area covered by each category in a barplot (visualised by a specific colour in Fig. 2) was divided by the total area, therefore representing the proportion of time spent in a category over a simulation run with a specific combination of parameter values (Figs 3–6).

In the absence of cross-boundary management, no metapopulation was classified as 'Not common' at the end of the simulations. Except for the minimum values of growth and dispersal rate, the majority of the simulations reached high abundance and occupancy, often quickly (i.e. the 'Successful' category, often transiting through the 'Highly Successful' category; Figs 3A, C, 4A, C). Under a Gaussian kernel and at low dispersal, populations were only present in a few patches, and reached high abundance with a speed depending on the per capita growth rate (i.e populations with low growth rate remained in the 'Newly established' category for a long time before transiting to the 'Constrained' category, via 'Incipient' when growth rate increased). As growth rate increased, simulations reached the 'Successful' category, because high local abundance provided propagules to disperse to other patches. For low growth rate and high dispersal, metapopulations dispersed quicker, reaching the 'Sparse + abundant somewhere' via the 'Dispersed' category. Very few simulations reached the 'Sparse' category, because population size in the initial patch increased over time. For high growth and dispersal rates, metapopulations first rapidly increased in occupancy, followed by their local abundance, and therefore reached 'Highly successful' via the 'Dispersed' and the 'Dispersed + abundant somewhere' category (Figs 3A, 4A).

Results were qualitatively similar for the Cauchy dispersal, as shown by the similar colour distributions (compare Fig. 3A, C). There were nonetheless quantitative differences, as the establishment of small populations in several patches within a short time

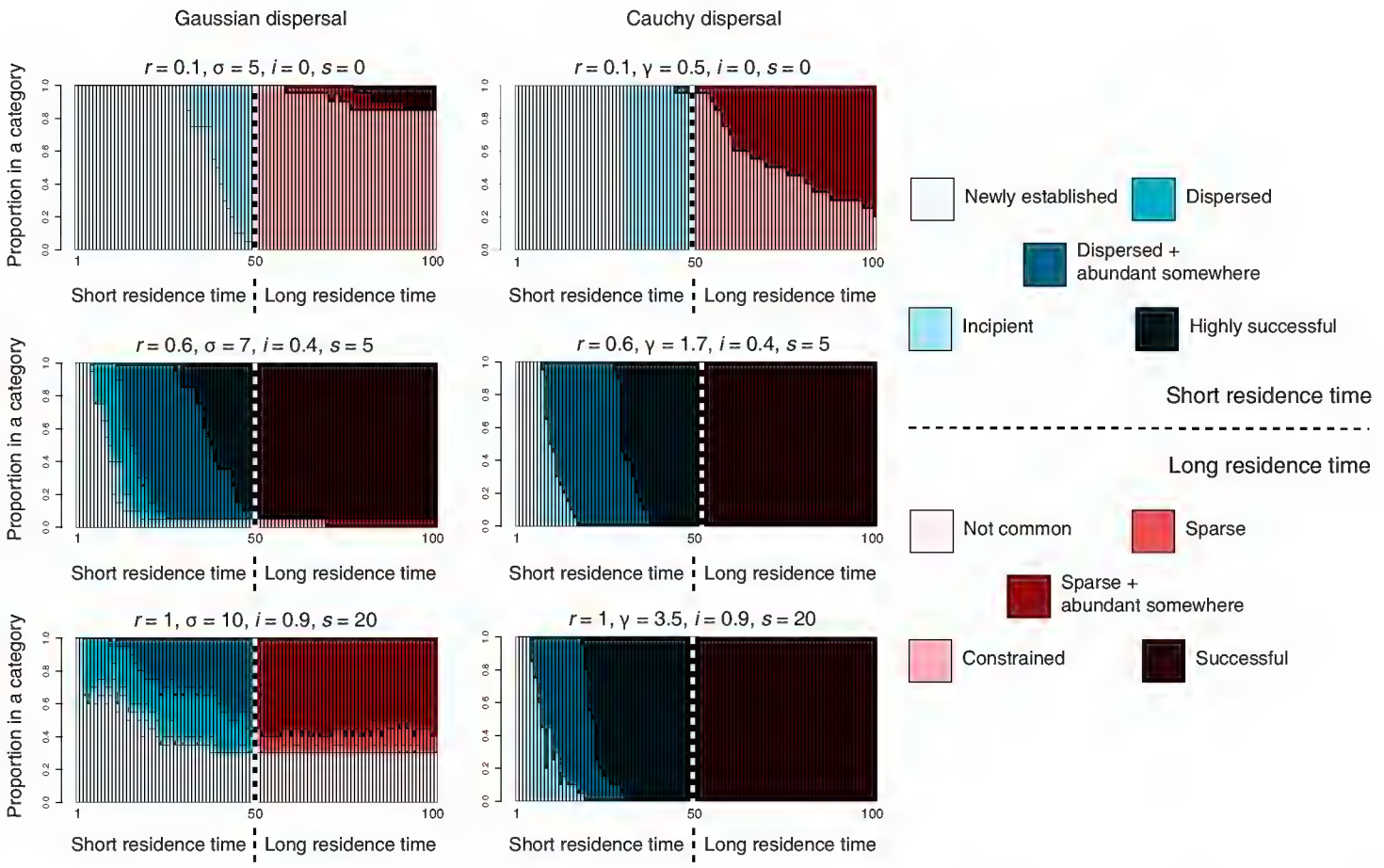
Gaussian dispersal
Cauchy dispersal
r = 0.1, σ = 5, i = 0, s = 0
r = 0.1, γ = 0.5, i = 0, s = 0
r = 0.6, σ = 7, i = 0.4, s = 5
r = 0.6, γ = 1.7, i = 0.4, s = 5
r = 1, σ = 10, i = 0.9, s = 20
r = 1, γ = 3.5, i = 0.9, s = 20
Proportion in a category
Short residence time
Long residence time
Newly established
Dispersed
Dispersed + abundant somewhere
Incipient
Highly successful
Short residence time
Long residence time
Not common
Sparse
Sparse + abundant somewhere
Constrained
Successful

Figure 2. Modelling the fate of alien species populations and their assignment to different categories of commonness through time for the Gaussian and Cauchy dispersal kernels, for specific combinations of per capita growth rate, dispersal capacity, interception efficacy and synchronisation of cross-boundary management (low, intermediate and maximum over the three columns), using the framework presented in Fig. 1. The lengths of the bars represent the proportion of simulations ending in a given category for a given time step, over the 20 replicates (each replicate being characterised by a different spatial distribution of the patches).

through long-distance dispersal events led to (i) more widespread populations with high local abundance (expressed by a higher proportion of time spent in the 'Dispersed + abundant somewhere', 'Highly successful' and 'Successful' categories), and (ii) very few simulations resulting in the 'Constrained' category (Figs 3C, 4C).

The impact of cross-boundary management on the trajectories to commonness

Cross-boundary management preventing the migration of propagules between patches had a much higher effect on populations with a Gaussian compared to those with a Cauchy dispersal kernel (compare the differences between Fig. 3A, B and Fig. 3C, D, between Fig. 4A, B and Fig. 4C, D; compare the changes in colours between Figs 5 and 6). In the case of Gaussian dispersal, interception efficacy was especially important, as shown by the variation in time spent in each category as interception efficacy increased and the fact that almost no population reached the 'Successful' category at high interception efficacy (Figs 3B, 4B; top row of the 'Successful' matrix in Fig. 5). As interception efficacy increased, populations became less widespread, but still had high

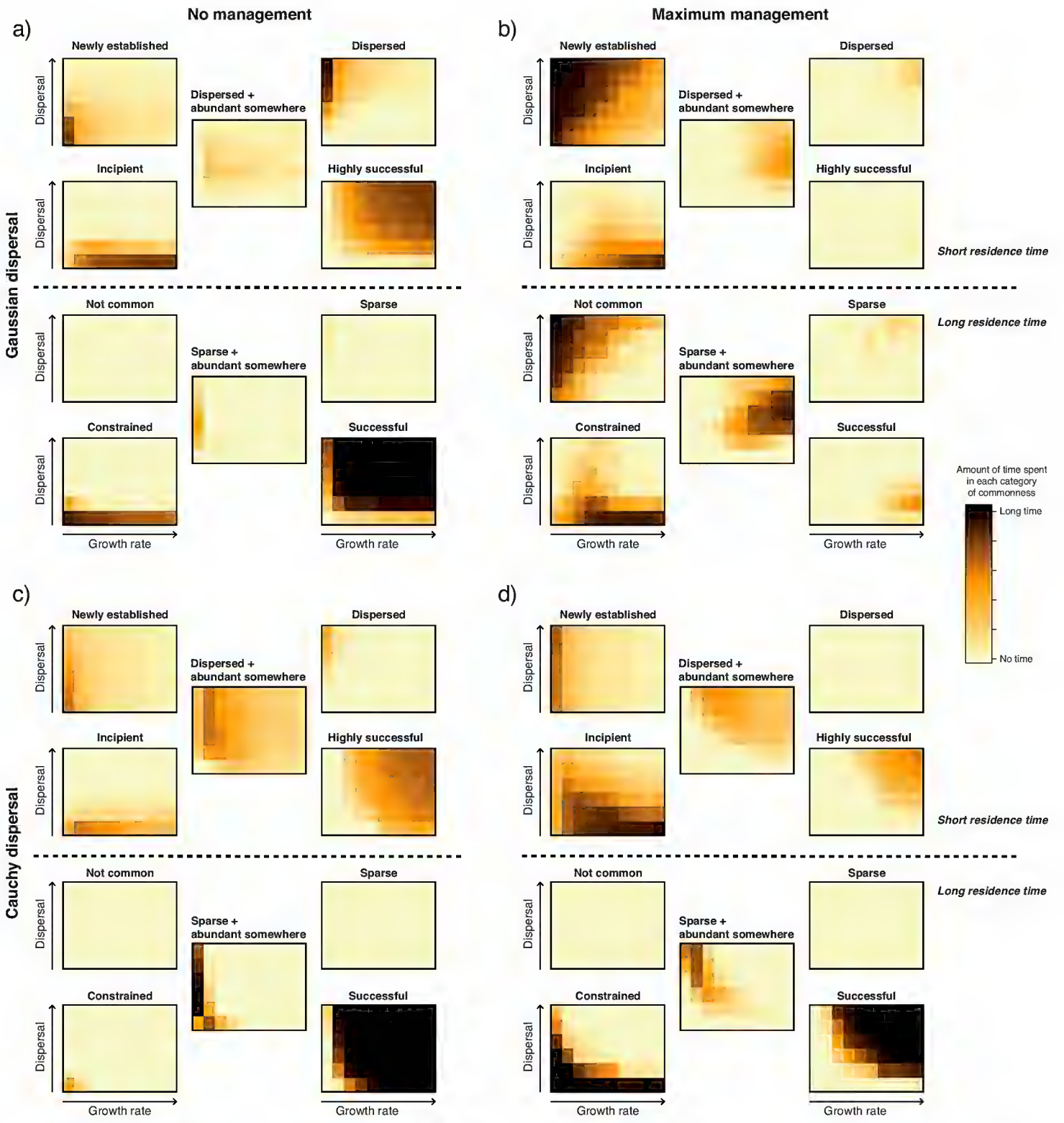

Figure 3. Modelling the fate of alien species populations with different population growth and dispersal rate, and their assignment to different categories of commonness, without (**a, c**) and with (**b, d**) maximum cross-boundary management (lowest and highest interception efficacy and synchronisation), for the logistic growth and the Gaussian (**a, b**) and Cauchy (**c, d**) dispersal kernels, using the framework presented in Fig. 1. Colours of the cells represent the proportion of time spent in each category of commonness for a specific combination of parameter values, with dark brown representing 50% of time and light yellow 0%. Simulations have been done for 20 patches with a carrying capacity K = 10 000, and the outputs were averaged over 20 replicates. Bottom-left corner is the lowest set of parameter values (see Table 1), representing low population growth and dispersal rate.

local abundance. This is reflected by the decline in the proportion of populations in the 'Successful' and 'Highly successful' categories, whereas the proportion of 'Newly established', 'Not common', 'Constrained' and 'Sparse + abundant somewhere' increased

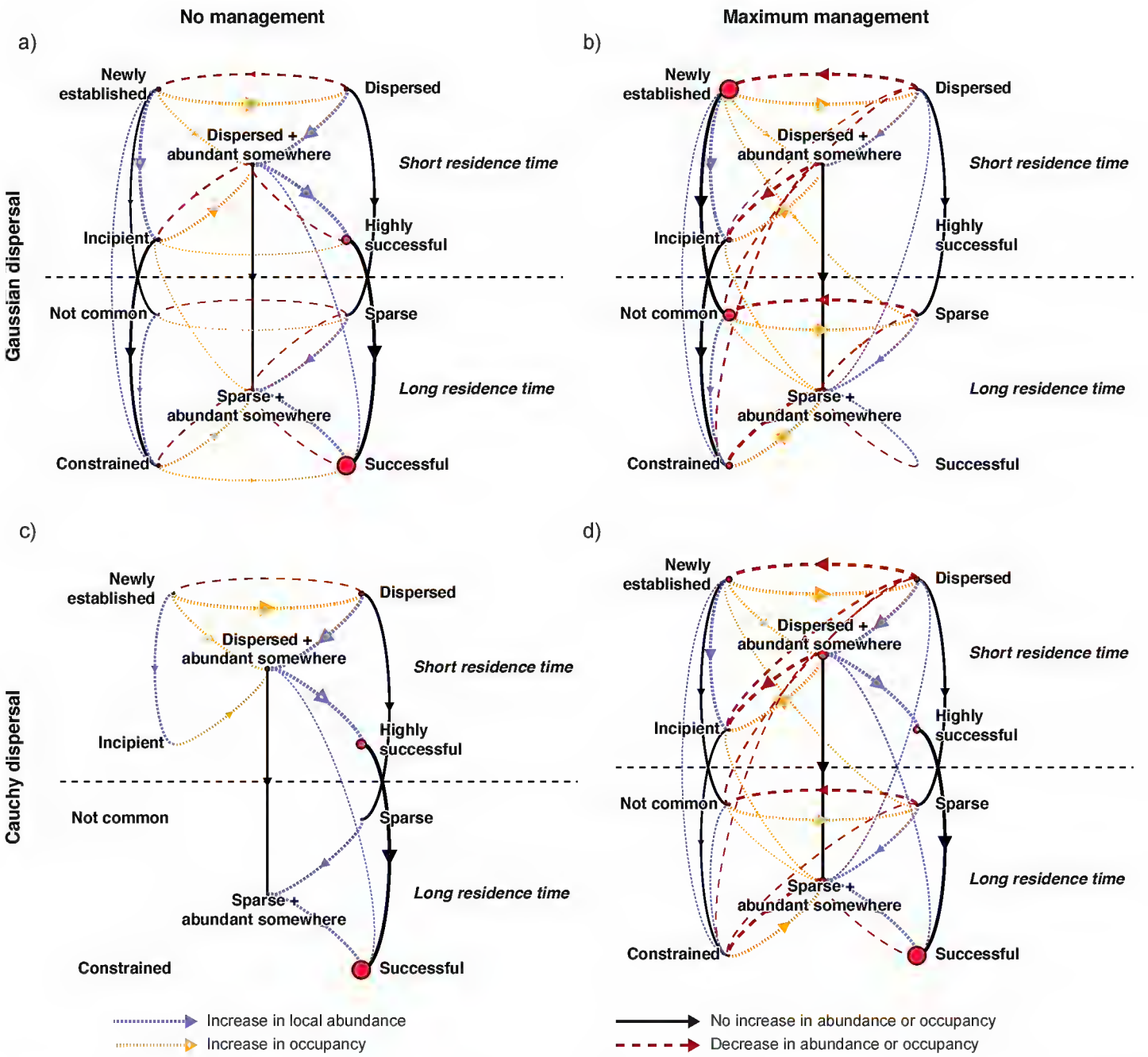

Figure 4. Transitions between different categories of commonness without (**a, c**) and with (**b, d**) maximum cross-boundary management (lowest and highest interception efficacy and synchronisation), for logistic growth, using the framework presented in Fig. 1, for the Gaussian (**a, b**) and Cauchy (**c, d**) dispersal kernel. Arrow width represents the frequency with which a metapopulation transited from one category to another, averaged over all combinations of growth and dispersal rate (i.e. averaging all cells in a matrix of Fig. 3). As in Fig. 1B, blue arrows represent an increase in local abundance, an orange represents an increase in occupancy, and black arrows represent no increase in either. Dark red arrows represent a decrease in either abundance or occupancy (which can happen as when abundance and occupancy values are close to the thresholds, and migrating propagules are intercepted). Simulations have been done for 20 patches with a carrying capacity K = 10 000, and the outputs were averaged over 20 replicates.

(moving up in the matrices of Fig. 5). The effect of synchronisation was only apparent at high interception efficacy, and had an important impact on the capacity of the species to become common, as shown by the large increase in time spent in the 'Newly established' and 'Not common' categories and a decline in the 'Dispersed + abundant

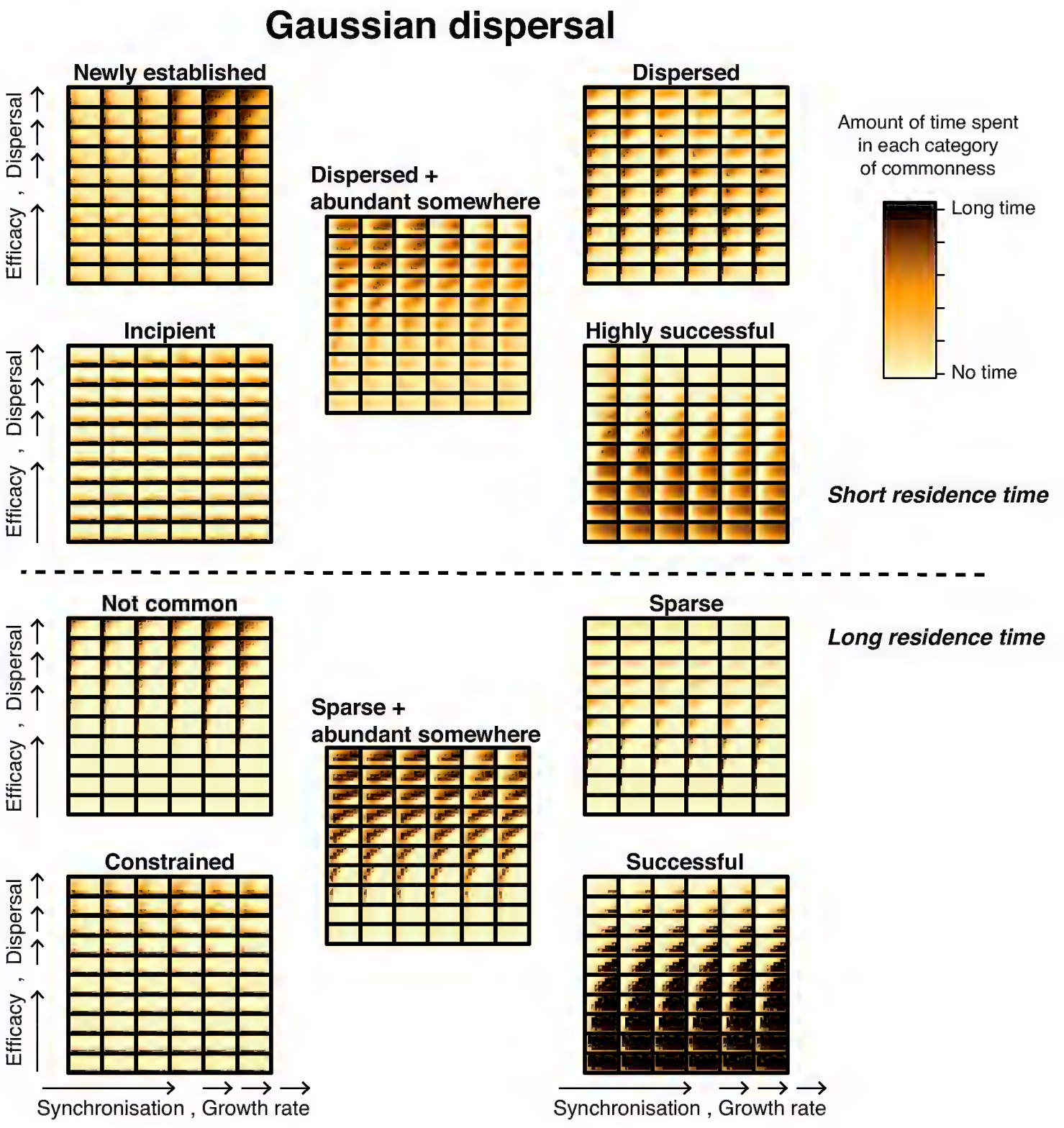

Figure 5. Effect of varying the interception efficacy and synchronisation of cross-boundary management for the Gaussian dispersal kernel on the fate of alien species populations and their assignment to different categories of commonness, using the framework presented in Fig. 1. Colours of the cells represent the proportion of time spent in each category of commonness for a specific combination of parameter values, with dark brown representing 50% of time and light yellow 0%. Results are presented so that variations in per capita growth and dispersal rates are nested within the synchronisation and efficacy of biosecurity measures. That is, within each category of commonness, each small rectangle represents a set of simulations for a given set of interception efficacy and synchronisation values. Within each small rectangle, the values of growth and dispersal rate are varied. Small rectangles in the bottom-left corners of each category of commonness are the lowest set of interception efficacy and synchronisation values, i.e. no cross-boundary management, and are the same as the matrices presented in Fig. 3A. Small rectangles in the top-right corners of each category of commonness are the highest set of interception efficacy and synchronisation values, and are the same as the matrices presented in Fig. 3B. Simulations have been done for 20 patches with a carrying capacity $K = 10\,000$, and the outputs were averaged over 20 replicates.

somewhere' and 'Sparse + abundant somewhere' categories (moving right in the top rows of the matrices of Fig. 5).

Although no within-patch management was implemented, cross-boundary management eventually caused species commonness to decline (dark red arrows in Fig. 4). This was a result of the effect of numerous migrating propagules being eliminated when dispersal was high, therefore countering demographic effects. This is also why, under high growth and dispersal rates, species reach the 'Sparse + abundant somewhere' rather than the 'Successful' category, the latter being mostly reached at intermediate dispersal rate (top-right of the corresponding matrices in Fig. 3B).

For the Cauchy dispersal kernel, cross-boundary management only had a substantial effect on population spread at high interception efficacy and high synchronisation (top-right of the matrices in Fig. 6). Contrary to the Gaussian dispersal kernel, for which the effect of interception efficacy was progressive, there was a threshold of 0.6 under which interception efficacy had no detectable effect (i.e. more than half of the propagules had to be intercepted; compare bottom and top halves of the matrices in Fig. 6). Once this threshold was attained, the effect of interception efficacy and synchronisation became apparent and was progressive, and mostly limited the spread of the metapopulation. Cross-boundary management then mostly increased the time spent in the 'Incipient' and 'Constrained' categories, and decreased the time spent in the 'Highly successful' and, to a lower extent, in the 'Dispersed + abundant somewhere' and the 'Successful' categories. However, with a Cauchy dispersal kernel even cross-boundary management with high interception efficacy and synchronisation had a limited effect on population spread and growth, and most simulations reached the 'Successful' and some even the 'Highly successful' categories (Figs 3D, 4D).

Variability in the results across the 20 replicates was much higher for the Gaussian than for the Cauchy dispersal kernel (compare Suppl. material 1: Figs C1 and C2 in Appendix C). The paucity of long-distance dispersal events when using the Gaussian kernel resulted in the spatial distribution of the patches being primarily responsible for the spread of an alien species. In contrast, the more likely long-dispersal events of the Cauchy dispersal kernels made the outcome of the simulations largely independent of the spatial distribution of patches.

The impact of time lags on the trajectories to commonness and the efficacy of cross-boundary management

Time lags in the growth rate of local populations led to increasing the time it took for the metapopulation to become common (compare Suppl. material 1: Fig. D5 in Appendix D with Fig. 2, Figs D2 and D4 with Fig. 5, and Figs D3 and D5 with Fig. 6). Using a weak Allee effect was similar to decreasing the growth rate for both dispersal kernels (compare Suppl. material 1: Figs D2 and D3 in Appendix D with Figs 5, 6). When a strong Allee effect was used, almost no simulation reached the 'Highly successful' or the 'Successful' categories, for both the Gaussian and the Cauchy dispersals

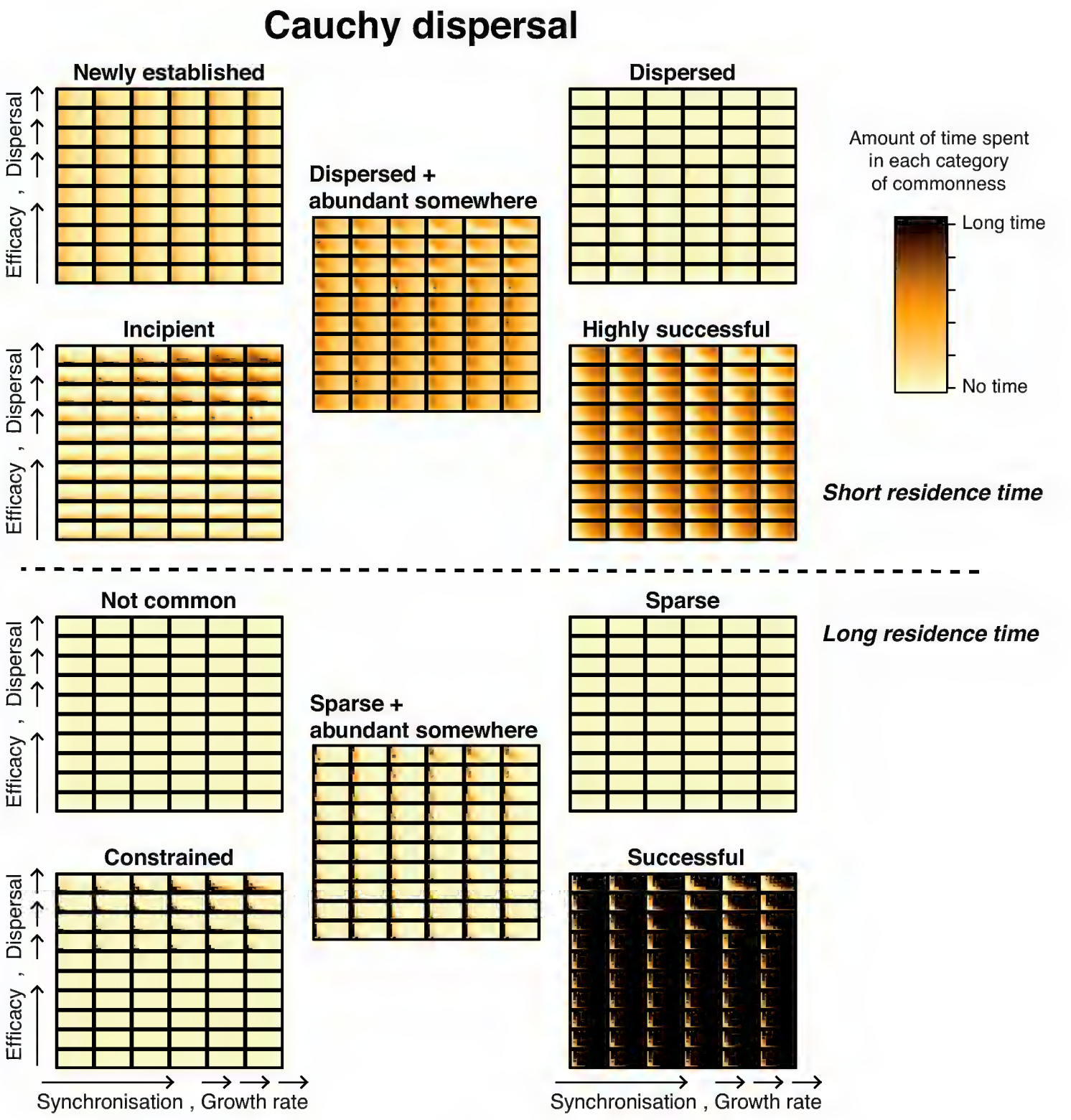

Figure 6. Effect of varying the interception efficacy and synchronisation of cross-boundary management for the Cauchy dispersal kernel on the fate of alien species populations and their assignment to different categories of commonness, using the framework presented in Fig. 1. Colours of the cells represent the proportion of time spent in each category of commonness for a specific combination of parameter values, with dark brown representing 50% of time and light yellow 0%. Results are presented so that variations in per capita growth and dispersal rates are nested within the synchronisation and efficacy of biosecurity measures. That is, within each category of commonness, each small rectangle represents a set of simulations for a given set of interception efficacy and synchronisation values. Within each small rectangle, the values of growth and dispersal rate are varied. Small rectangles in the bottom-left corners of each category of commonness are the lowest set of interception efficacy and synchronisation values, i.e. no cross-boundary management, and are the same as the matrices presented in Fig. 3C. Small rectangles in the top-right corners of each category of commonness are the highest set of interception efficacy and synchronisation values, and are the same as the matrices presented in Fig. 3D. Simulations have been done for 20 patches with a carrying capacity $K = 10\,000$, and the outputs were averaged over 20 replicates.

(Suppl. material 1: Figs D4 and D5 in Appendix D). For the Cauchy kernel, simulations that reached the 'Successful' category for logistic growth instead reached the 'Sparse + abundant somewhere' category for the strong Allee effect. For the Gaussian kernel, almost all simulations reached either the 'Not common' or the 'Sparse' category, depending on a threshold in the dispersal parameter.

When a weak Allee effect was used to model time lags, the general effect of cross-border management measures was similar to their application to metapopulations with logistic growth (compare Suppl. material 1: Figs D2 and D3 in Appendix D with Figs 5, 6). For the strong Allee effect and the Cauchy dispersal, a threshold of 0.5 on the interception efficacy over which an effect could be noted was observed, similar to metapopulations with a logistic growth and a weak Allee effect (compare Suppl. material 1: Fig. D5 in Appendix D with Fig. 6). In contrast, a threshold on the interception efficacy appeared for the Gaussian dispersal (Suppl. material 1: Fig. D4 in Appendix D). Over 20% of intercepted propagules, most simulations only reached the 'Not common' category (and to a lower extent the 'Sparse' category), which was not observed for the logistic growth and the weak Allee effect.

The effect of cross-boundary management also tended to be disproportionately higher for populations with time lags compared to logistic growth, for both the weak and strong Allee effects. The difference in ratios used to compute the relative effect was negative for the 'Highly successful' and 'Successful' categories (indicating disproportionally less time spent in these categories), and overall positive for the other categories, for both the Gaussian and the Cauchy dispersal (Suppl. material 1: Figs E1–E4 in Appendix E). The only exception was the 'Sparse + abundant somewhere' category for the Gaussian dispersal and weak Allee effect, as the time spent in this category was relatively lower with time lags at low growth rate values, and relatively higher at intermediate growth rate values.

Discussion

Effects of cross-boundary management on the trajectories to commonness

This study offers four key insights relevant to the prevention of the spread of alien species across borders of spatial entities (such as countries). First, the large difference in the impact of cross-boundary management on populations with versus without long-distance dispersal suggests that the implementation of preventive measures at the points of entry of a country (eg. at land borders, ports or airports) is unlikely to be efficient for all species. Global connections are increasing, both through trade of goods and movement of people, and preventing such long-distance distance transport of propagules across countries seems unrealistic under the current status-quo (McNeely 2006). It will therefore be important to evaluate how combinations of cross-border management with a range of local management measures (including biocontrol, culling, etc.) will enhance their respective efficiency. Since in our model, cross-border management had

a disproportionate effect when time lags were present, this suggests that this combination of ecological dynamics and management intervention may reinforce each other and could be deployed to improve management effectiveness by control measures that simulate a lag effect, i.e. reducing population reproductive output by, for example, biological or other forms of control.

Second, interception efficacy of cross-boundary management has a larger effect on the capacity of a metapopulation to become more common than synchronization between regions, over the range of parameters for which cross-border management has an effect on the spread of the metapopulation. Increasing interception efficacy decreased the growth of metapopulations, which therefore reached the 'Highly successful' and 'Successful' categories less frequently, regardless of the synchronisation between countries, in the absence of long-distance dispersal (i.e. for the Gaussian dispersal kernel). Synchronisation only had a noticeable effect when more than half of the propagules entering a patch were consistently intercepted. When long-distance dispersal occurred (i.e. for the Cauchy dispersal kernel), a combination of both high interception efficacy and good synchronisation between countries was required to substantially limit the ability of the population to become 'Highly successful' or 'Successful', although that only applied for low growth rate and dispersal capacity.

Importantly, there was a clear threshold indicating that at least half the propagules entering a patch were required to be intercepted consistently to prevent the metapopulation from dispersing rapidly (Figs 5, 6). These results suggest that implementing effective national biosecurity measures have the potential to limit the spread and growth of alien species even if other countries are lagging behind in their implementation, but that their efficacy will likely be enhanced if they are implemented simultaneously by multiple countries. Doing so is necessary to prevent the emergence of small, separate populations of alien species, whose detection and eradication has been shown to be more important than that of large populations (Mack and Lonsdale 2002). This result provides support for the importance of the species-targeted, cross-boundary control efforts for invasive alien species of agricultural and environmental concern that have been advocated elsewhere (Epanchin-Niell and Hastings 2010; Kark et al. 2015; Blackburn et al. 2020).

Third, the spatial distributions of the patches had a stronger effect on the time spent in each category of commonness for the populations without long-distance dispersal, as shown by the higher standard deviation in each category (Suppl. material 1: Figs C1–C6 in Appendix C). For populations whose spread follows a diffusion process and which increase their local abundance before spreading to neighbouring regions, cross-boundary management limiting immigration to a new patch is probably not the most efficient management, especially without clear spatial planning. Such spatial planning can be difficult to achieve across different countries with their own constraints and priorities. Instead, early detection combined with removal actions (see e.g. Travis and Park 2004; Chadès et al. 2011 for guidelines on the spatially-explicit management of alien species) or cross-boundary management limiting the emigration from a location where the species is present, may be more efficient. For example, the International Standards for Phytosanitary Measures No. 15 (ISPM15), developed by the International Plant Protec-

tion Convention, provides treatment standards for wood packaging materials, to limit the introduction of alien wood-feeding insects (Haack et al. 2014). The Ballast Water Management Convention ensures that ships from signatory countries perform ballast water replacement at least 200 nautical miles from shore, and use approved ballast water treatment systems, to prevent carrying and spreading aquatic alien species (IMO 2004).

Finally, the disproportionately beneficial effects of cross-border management when time lags were implemented in the model suggests that preventive cross-boundary management may provide a substantial advantage to contain the spread and growth of undetected alien species undergoing time lags. Time lags have been shown to impair the prediction of future invasions, therefore impeding proper application of management actions (Taylor and Hastings 2005). However, the relationship between cross-boundary management and time lags is often neglected (see e.g. table 1 in Tobin et al. 2011).

Application of the categories of commonness

Establishing the link between the categories of commonness, species biology, cross-boundary management and *in situ* management measures could improve our ability to understand and therefore to limit the spread of alien species, and therefore their potential impact. The combination of the typological framework with the modelling approach presented here enables exploration of the effects of different levels of interception efficacy and synchronisation of cross-boundary management across different regions, and for species with different demographic and dispersal characteristics.

Applying the framework to a theoretical model setting has shown unexpected results for the path to commonness of populations with different demographic and dispersal characteristics. In particular, the results demonstrate that dispersal can be so high that, combined with very efficient cross-boundary management, this could result in the metapopulation becoming less common than under lower dispersal rates, for the Gaussian dispersal kernel (as shown by the dark colour in the bottom-left of the small squares in the 'Successful' matrix in Fig. 5). Although these simulations are less realistic than other combinations of parameter values, they can be used to conceptualise specific situations. Very high dispersal despite low abundance in the model can represent the existence of hubs through which propagules transit (Floerl et al. 2009). Very high dispersal rate and very efficient cross-boundary management in the model, leading to a decrease in overall abundance, can represent the combination of additional management actions of species already established (Novoa et al. 2018; Martin et al. 2020). In addition, only two types of dispersal kernels, representing a diffusion process and long distance dispersal, were implemented in the model to simplify the analyses and due to computational limitations. In practice, both types of dispersal would therefore occur simultaneously in a metapopulation, with the exact shape of their kernel and their relative rate depending on the species biology and the characteristics of the environment (Pyšek and Hulme 2005). Our simulations were designed to represent two extreme cases between which real species' spread will lie.

In the theoretical model presented here, the time period spent by a population in each category of commonness will be influenced by the parameter values, the number

of patches available, the carrying capacity of the patches, and their spatial distribution (Alharbi and Petrovskii 2019). In particular, using parameter values for the two dispersal kernels that allow for a comparison of the results is not straightforward, and we used a visual inspection of the kernels to do so. The thresholds to differentiate the 10 types of commonness were then determined so that each category of commonness would be represented in the simulations. This enabled us to better detect the effect of different cross-boundary management measures on the path to commonness for the two extreme types of dispersal models and the set of parameters used in the simulations.

In practice, thresholds should be based on the biology and the ecology of species (for example on the species ability to maintain stable populations). Using such criteria would allow for global assessments of the state of biological invasions, as is done, for example for species becoming rare with the IUCN Red List of Threatened Species (IUCN 2019). From an applied management perspective, defining the thresholds based on the management capacity of countries may also be appropriate, and could vary in space and time based on the management capacities of a country, the development of novel management methods, and an understanding of how the 'coupled human and natural system' affects invasions (Sinclair et al. 2020).

The model we used therefore represents a canvas on which more realistic and specific models can be based. Such models can be based on the parameterisation of the growth and dispersal rate of specific species (including a more progressive exploration of changes in the frequency of long-distance dispersal events). They can also explore how the spatial distribution, size distribution and environmental heterogeneity of multiple countries can be analysed using this framework of categories of commonness.

Conclusions

Understanding the trajectories of alien species introduced into separate spatial units (e.g. countries, islands, water bodies) that ultimately may lead to commonness is crucial for designing effective management measures. Appreciating that IAS become abundant and expand their ranges in a number of distinct ways provides potential to explore options for designing the most effective, category-specific management strategies (Novoa et al. 2020). The typological framework presented here enables us to analyse the role of cooperation among spatial units for altering how a newly introduced species may become common across them. The theoretical model was designed to be adapted to real systems in the future, including cross-border surveillance, biosecurity or legislation such as the EU regulation on invasive alien species (EU 2014). We consider the following insights particularly relevant for applied purposes: First, spread will be reduced more if some countries implement effective biosecurity, albeit interceptions are not rapidly implemented everywhere (i.e. low management synchronisation but high efficacy) rather than all countries implementing biosecurity at the outset but the rate of interceptions is low (i.e. high management synchronisation but low efficacy). Second, the presence of long-distance dispersal requires a minimum level of interception efficacy to prevent an alien species from becoming common across a set of spatial units, although that only applied for low growth rate

and dispersal capacity. Once such a threshold is crossed, synchronisation across spatial units will improve the efficacy of management. Third, time lags in population growth that may result in delayed spread are an important aspect to be considered explicitly for management, as they can amplify the efficacy of such measures. It will be important to assess the generality of these findings for a range of different real cases.

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Supplementary material I

Appendix A–E

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Data type: Supplementary documentation

Explanation note: **Appendix A.** Archetypes of trajectories to commonness; **Appendix B.** Model characteristics; **Appendix C.** Standard deviation results without time lags; **Appendix D.** Results with time lags; **Appendix E.** Relative effect of pre-border cross-boundary management for the Gaussian dispersal kernel with and without time lags.

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